Received: 22 September 2017 | Accepted: 26 January 2018

DOI: 10.1111/1365-2745.12961

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

INTRANSITIVE COMPETITION AND SPECIES COEXISTENCE

Emergence of weak-intransitive competition through adaptive diversification and eco-evolutionary feedbacks

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Funding information
DST-NRF Centre of Excellence for Invasion Biology and National Research Foundation of South Africa, Grant/Award Number: 85417, 89967 and 109244

Handling Editor: Eric Allan

Abstract

1. Indirect biotic interactions—such as intransitive competition—are increasingly recognized as being important in shaping ecological patterns in natural systems. Over long time-scales, such indirect interactions may affect the evolution of species phenotypes, which in turn can modify these interactions, thereby begetting eco-evolutionary feedbacks. If indirect intransitive interactions can emerge in situ during lineage diversification, they could profoundly affect species' phenotypic diversity, temporal stability, and subsequent diversification rates.
2. We address these questions by investigating the conditions under which indirect intransitive competition can emerge from a lineage diversifying in sympatry. We use an adaptive dynamics model to study the ecological and evolutionary properties of this lineage under different scenarios where competition for resources between phenotypes varies in strength and (a)symmetry.
3. Results show that *weak-intransitive competition* can emerge during the sympatric diversification of a single lineage. "Weak-intransitivity" here refers to situations where species interactions are not perfectly transitive, that is, there is no strict hierarchy in species competitive abilities. The strength of such weak-intransitivity increases when the competition between phenotypes increases in strength and asymmetry. The strength of intransitivity also correlates with other system properties. We notably found that the strength of intransitivity increases with the number of phenotypes, and that greater intransitivity correlates with the evolution of greater functional trait divergences between phenotypes, greater resistance to invasion by new phenotypes but lower resistance to disturbances as well as slower evolutionary rates.
4. *Synthesis*. This theoretical exploration of the evolution of intransitive competition provides the first formal bridge between the ecological and evolutionary aspects of intransitive competition. We show that, when competitive interactions are strong enough, weak-intransitive competition is more likely to emerge through adaptive diversification than from a random community assembly. Intransitive competition is, therefore, not only restricted to between-species interactions but can also function as a regulator of diversification within species, thereby affecting lineage functional diversity, and ecological and evolutionary stability.

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KEYWORDS
adaptive dynamics, asymmetric competition, coexistence theory, community stability, evolutionary branching, Lotka–Volterra competition model, rock–paper–scissors competition

1 | INTRODUCTION

At the scale of local plant communities, species coexistence is generally limited by competitive interactions. The competitive effect of one species on another can be either direct or, when mediated by multispecies interaction chains, indirect (Levine, 1976; Wootton, 1994). Although often neglected, indirect interactions have been shown to be frequent in natural plant communities (e.g. Mayfield & Stouffer, 2017; Soliveres et al., 2015; Wootton, 2001) and to have important impacts on species coexistence (Allesina & Levine, 2011; Vandermeer, 2011).

Among indirect interactions, intransitive competition has special importance. Intransitive competition, also called cyclic competition, occurs when the competitive superiority of species is not strictly hierarchical (as in the "rock-paper-scissors" game). For example, in a hypothetical community with three species {A, B, C}, an intransitive loop of competitive interactions emerges if A is a better competitor than B (denoted as A > B hereafter), B is a better competitor than C (B > C) and C is a better competitor than A (C > A, thus A > B > C > A; Gilpin, 1975; May & Leonard, 1975). Over ecological time-scales, intransitive loops can have important stabilizing or destabilizing effects on species coexistence. Indeed, if the loop comprises an odd number of species, it can induce negative frequency-dependent population growth and thus promote species coexistence (Allesina & Levine, 2011; Durrett & Levin, 1998; Hui, Li, & Yue, 2004; Huisman & Weissing, 1999). On the other hand, if the loop comprises an even number of species, then small disturbances can be amplified by the loop, resulting in the destabilization of species coexistences, potentially driving one or more species to local extinction (Gallien, Zimmermann, Levine, & Adler, 2017). Furthermore, because intransitive competition emerges from cyclic species hierarchies, it can generate random-like patterns in functional diversity at the level of the community; this is in contrast to what is usually expected from direct competitive interactions (Gallien, 2017; but see interesting spatial patterns of species distribution in Reichenbach, Mobilia, & Frey, 2007; Zhang, Li, & Hui, 2006).

Most studies of intransitive competition undertaken to date have been conducted at the scale of the community and have considered only interspecific interactions. However, a few empirical studies suggest that intransitive competition can also emerge within lineages as a form of *intraspecific intransitive competition*, thus acting to structure the phenotypic diversity of a given species' population. It has, for example, been shown that conspecific populations containing three phenotypes competing for resources in an intransitive fashion could coexist stably in nature (e.g. Sinervo & Lively, 1996 in lizards; Rainey & Travisano, 1998 in bacteria). Such empirical evidence raises the question of whether intraspecific intransitive competition has evolved locally from a single original phenotype or whether it results from the assembly of already differentiated phenotypes. In other words, can intraspecific intransitivity emerge from sympatric phenotypic diversification, or does it require the immigration and assembly of already differentiated phenotypes? If intraspecific intransitive competition can emerge in situ, such a mechanism may not only be frequent in nature at the community scale but also at the population scale. Furthermore, given the ecological effects of intransitive competition on the stability of coexistence, and functional diversity at the community scale, its emergence and evolution within a lineage may create eco-evolutionary feedback loops with potential long-term consequences for lineage evolution (Ferrière & Legendre, 2013). Such eco-evolutionary feedbacks would for instance happen when the individuals of a plant species are characterized by inheritable phenotypes (e.g. height at maturity and tolerance to shade), and when these phenotypes also influence the local environment (e.g. the taller phenotypes intercept more light) in a way that favours the persistence of mutants (e.g. mutant individuals with greater height and/or greater tolerance to shade have a higher fitness). Understanding the evolutionary facets of such a mechanism is therefore important to identify potential relationships between intransitive competition and the dynamics and maintenance of polymorphism within species.

The evolutionary origins of intransitive competition have remained largely unexplored. There are two likely reasons for this: (1) the limited number of tools for studying eco-evolutionary feedbacks in a competition context and (2) the absence of metrics for capturing or detecting the emergence of intransitive competition at a very early stage. The first limitation can be overcome using a promising tool: theoretical adaptive dynamics (AD) models which were specifically designed to explore eco-evolutionary feedbacks (Dieckmann, O'Hara, & Weisser, 1999; Ferrière & Legendre, 2013; Metz, Geritz, Meszéna, & Jacobs, 1996). These models have the additional advantage that they can integrate trait-based competitive interactions in the standard Lotka–Volterra competition model (where the strength of competition is assumed to be phenotype dependent; Calcagno, Jarne, Loreau, Mouquet, & David, 2017; Doebeli & Dieckmann, 2000). Such Lotka–Volterra models have been widely used for studying plant coexistence and succession dynamics both empirically and theoretically (e.g. Chesson, 2000a, 2000b; Godoy, Kraft, & Levine, 2014; Levine & HilleRisLambers, 2009; Mayfield & Stouffer, 2017). Secondly, to be able to track the emergence of intransitive competition, it is crucial to detect this interaction as soon as it appears, even though it may show only a weak signal. Indeed, competitive interactions can take various forms and strengths, ranging from strongly transitive (A excludes B and C, B excludes C) to strongly intransitive (A excludes B, B excludes C, C excludes A). Interaction transitivity

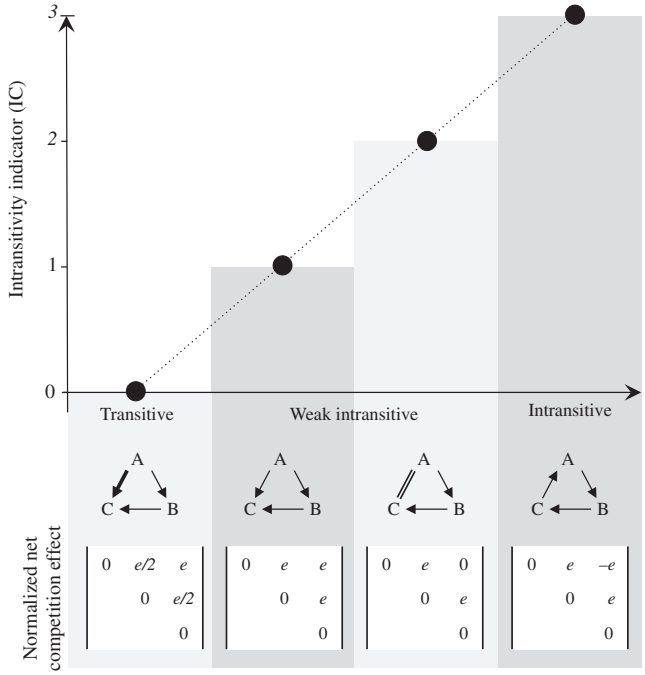

FIGURE 1 Illustration of the intransitivity indicator (IC) measuring the degree of intransitivity along the transitive-to-intransitive continuum for three interacting phenotypes {A, B, C}. The index is based on the matrix of normalized net competition effects (see below, where $0 \leq |e| \leq 1$), which can also be represented with a directed network (where arrows point towards the weaker competitors, arrow width indicates the strength of the interactions and double lines indicate no or equal competitive interactions). Notice that in cases of very strong transitivity, the index can also be negative (not shown)

is maximal between three species (A, B, C; where A > B > C) when the net effect of A on C is equal to the sum of the net effects of A on B and of B on C; while interaction intransitivity (A > B > C > A) is maximal when the net effect of A on B equals the net effects of B on C and of C on A (Figure 1). Many intermediate cases of "weaker" interactions can also occur between these extreme transitive and intransitive interactions. This can typically happen when the interaction between two of the three species weakens (for instance when the net effect of A on C tends toward zero: (A > B > C = A; Keddy & Shipley, 1989). Since these "weaker" interactions are not transitive sensu stricto, we hereafter refer to them as "weak-intransitivity" (Figure 1). To capture the continuous nature of (in)transitivity, we designed a new standardized index that can quantify the level of (in) transitivity in species interaction.

This paper tackles a central question: *Can intraspecific intransitive competition evolve locally from a single original phenotype?* We address this question by applying an AD model initiated with a population containing one single phenotype, which—via frequency-dependent disruptive selection driven by resource competition (i.e. selection favouring extreme phenotypes over intermediate ones to reduce niche overlap and thus competition)—may diversify into multiple coexisting phenotypes that may or may not interact intransitively. Equipped with this model and with a new index for detecting and quantifying early signals of intransitivity, we investigate whether and, if so, then under which conditions intraspecific intransitive competition can emerge from a monomorphic lineage. Specifically, we explore how the type and magnitude of competition (from purely symmetric to strongly asymmetric competition) affect (1) the emergence of intransitivity, (2) the phenotypic diversity of the evolving lineages, (3) the stability of their coexistence and (4) their divergence rates. Our study provides the first formal bridge between the ecological and evolutionary aspects of intransitive competition, a mechanism potentially occurring not only between but also within species.

2 | MATERIALS AND METHODS

2.1 | Modelling adaptive dynamics

2.1.1 | Trait-mediated ecological dynamics

We use the adaptive dynamics (AD) model of asymmetric competition introduced by Doebeli and Dieckmann (2000; see Box 1 and Appendix S1 for details). In this AD model, individuals compete for resources through one scalar trait x (e.g. shoot/root biomass ratio, where high values indicate high light interception but limited access to nutrients; Dybzinski, Farrior, Wolf, Reich, & Pacala, 2011), which is assumed to be a continuous variable (possibly obtained through a nonlinear scaling, e.g. logarithmic). For simplicity, the model only handles resources implicitly by imposing a trait-dependent carrying capacity function (if we follow our trait example of shoot/root biomass, the resources may then be light/nutrient ratio in the environment). The carrying capacity is represented by a Gaussian function (of width σ_K) along the trait axis, $K(x) = K_0 \exp\left(-\frac{(x-x_0)^2}{2\sigma_k^2}\right)$, characterized by a single maximum K_0 around an optimal trait x_0 (we assume $K_0 = 1$ and $x_0 = 0$ without loss of generality).

Competition for resources is trait-mediated and asymmetric: individuals with larger trait values are better competitors than those with smaller values. However, this increase in competitive ability with trait values eventually comes at a cost of a smaller carrying capacity ($K(x)$ declines with x when $x > x_0$). This generates a competition trade-off, similar to what occurs in nature when the competitive ability of species correlates negatively with their resource consumption or growth rates (e.g. large investment in plant aboveground biomass increases competitive ability for light interception but reduces the investment in below-ground biomass and thus access to soil resources; Dybzinski et al., 2011). Competition strength also declines with increasing trait differences between phenotypes. This trait-mediated asymmetric competition of phenotype y on phenotype x (identical to the competition coefficient α_{xy} in a standard Lotka–Volterra model) is defined by the following function (see Box 1 and Appendix S1),

$$\alpha(x-y) = \exp\left(\frac{-(x-y)^2}{2\sigma^2}\right) / \exp\left((x-y)\,\beta\right) \quad (1)$$

where x and y represent the trait values of two lineages, while σ and β describe the strength and asymmetry of competition. For a pair of

phenotypes with traits x and y, a greater value of σ amplifies their niche overlap, resulting in an increased competition coefficient α. A greater value of β gives more advantage to the larger competitor over the smaller competitor. The intra-phenotypic competition coefficient $\alpha(x-x)$ is 1, so that the phenotype reaches its carrying capacity $K(x)$ in the absence of competition from other lineages (see Appendix S1).

2.1.2 | Trait adaptive dynamics

The population initially comprises a monomorphic lineage characterized by its trait x. Mutation and selection drive the trait evolution of the lineage, with the fate of mutants being determined by their *invasion fitness* (Metz, Nisbet, & Geritz, 1992). A mutant is characterized by its trait y and invasion fitness:

$$f(x,y) = r\left(1 - \frac{\alpha(y-x)K(x)}{K(y)}\right) \quad (2)$$

where r is the trait-independent intrinsic growth rate, and $K(x)$ and $K(y)$ are the carrying capacities attainable with traits x and y respectively. The invasion fitness thus represents the per capita growth rate of a nascent lineage of trait y competing with the resident phenotype(s) sitting at equilibrium abundance(s). If the invasion fitness of the mutant is higher than the fitness of the resident phenotype, the mutant can competitively exclude this resident, thus changing the resident trait from x to y, making one incremental step of evolution (see Box 1). Trait evolution proceeds with a succession of mutant-resident substitutions along the *selection gradient*, $g(x) = r\left(\beta - \frac{x}{\sigma_k^2}\right)$ (Dieckmann & Law, 1996; for more details, see Appendix S1). Such directional selection will continue until an evolutionary equilibrium is reached ($\bar{x} = \beta\sigma_k^2$), representing either a local maximum or minimum in the fitness landscape. A local fitness maximum signals the end of incremental evolution, whereas a local fitness minimum (happening when $\sigma < \sigma_K$) begets *evolutionary branching*. Evolutionary branching allows the resident and mutant to coexist, forming two resident phenotypes diverging under disruptive selection (Della Rossa, Dercole, & Landi, 2015; Dercole, Della Rossa, & Landi, 2016; Geritz, Kisdi, Meszéna, & Metz, 1998). After a branching event, trait evolution continues separately in each lineage, where further branching events are possible (Landi, Dercole, & Rinaldi, 2013). Trait-mediated competition in the above model can affect the population sizes at equilibrium, which then alters the density-dependent fitness and thus the selection gradient. Such altered selection force dictates how traits can be replaced from incremental mutation along the selection gradient and thus the trajectory of trait evolution. This forms an eco-evolutionary feedback loop that affects the population dynamics by interfering in the strength of trait-mediated competition (see Box 1; Fussmann, Loreau, & Abrams, 2007). Since each lineage develops a distinct phenotype, we use the words *lineage* and *phenotype* interchangeably from here on.

2.1.3 | Model simulations

Our aim with using the AD model was to determine whether, and if so then under which conditions, intransitive competition could emerge from sympatric evolution. To do so, we compared simulations of phenotypic evolution and diversification under different scenarios of pairwise competitive interactions. The scenarios were

BOX 1 Eco-evolutionary feedbacks and adaptive dynamics model

Adaptive Dynamics (AD) is a theoretical framework for studying phenotypic changes that take place over time in evolving populations (Dercole & Rinaldi, 2008; Waxman & Gavrilets, 2005) and relies on the interplay of ecological and evolutionary dynamics (Figure S1). In AD, populations are characterized by individual traits, which determine the ecological interactions among populations (e.g. competition) and thus their coexistence. Together, these coexisting populations define the local biotic environment, which can then induce phenotypic evolution by imposing a selective pressure on the adaptive traits to increase individual fitness. Under certain conditions, such eco-evolutionary feedback loop can lead to evolutionary branching.

Here, we used the AD model of asymmetric competition introduced by Doebeli and Dieckmann (2000), in which individuals compete for resources through one trait x (e.g. shoot/root biomass ratio). Competition for resources is described by a trait-mediated version of the standard Lotka–Volterra competition model (see Eq. (1) and competition function in Figure Box.a), while the adaptive dynamics of the phenotype(s) into consideration is determined by the ecological growth rate of rare mutant phenotypes into the biotic environment set by the resident traits (also called *invasion fitness*; see Eq. (2) and Appendix S1 for more details). At the start, a monomorphic population will typically undergo directional trait evolution (i.e. replacement of the resident trait by the mutant trait with positive invasion fitness) until it reaches an evolutionary equilibrium (i.e. null fitness gradient; Figure Box.b). Then, at this equilibrium, evolutionary branching may take place if the resident phenotype can coexist with a new mutant phenotype and their traits undergo disruptive (rather than stabilizing) selection, leading to a new sequence of dimorphic directional evolution (Figure Box.c). Classic adaptive dynamics thus directly applies to organisms reproducing asexually (e.g. clonal plants), but its results have been shown generalizable to sexually reproducing organisms under broad conditions (Dieckmann & Doebeli, 1999; Geritz & Kisdi, 2000).

(Continues)

BOX 1 (Continued)

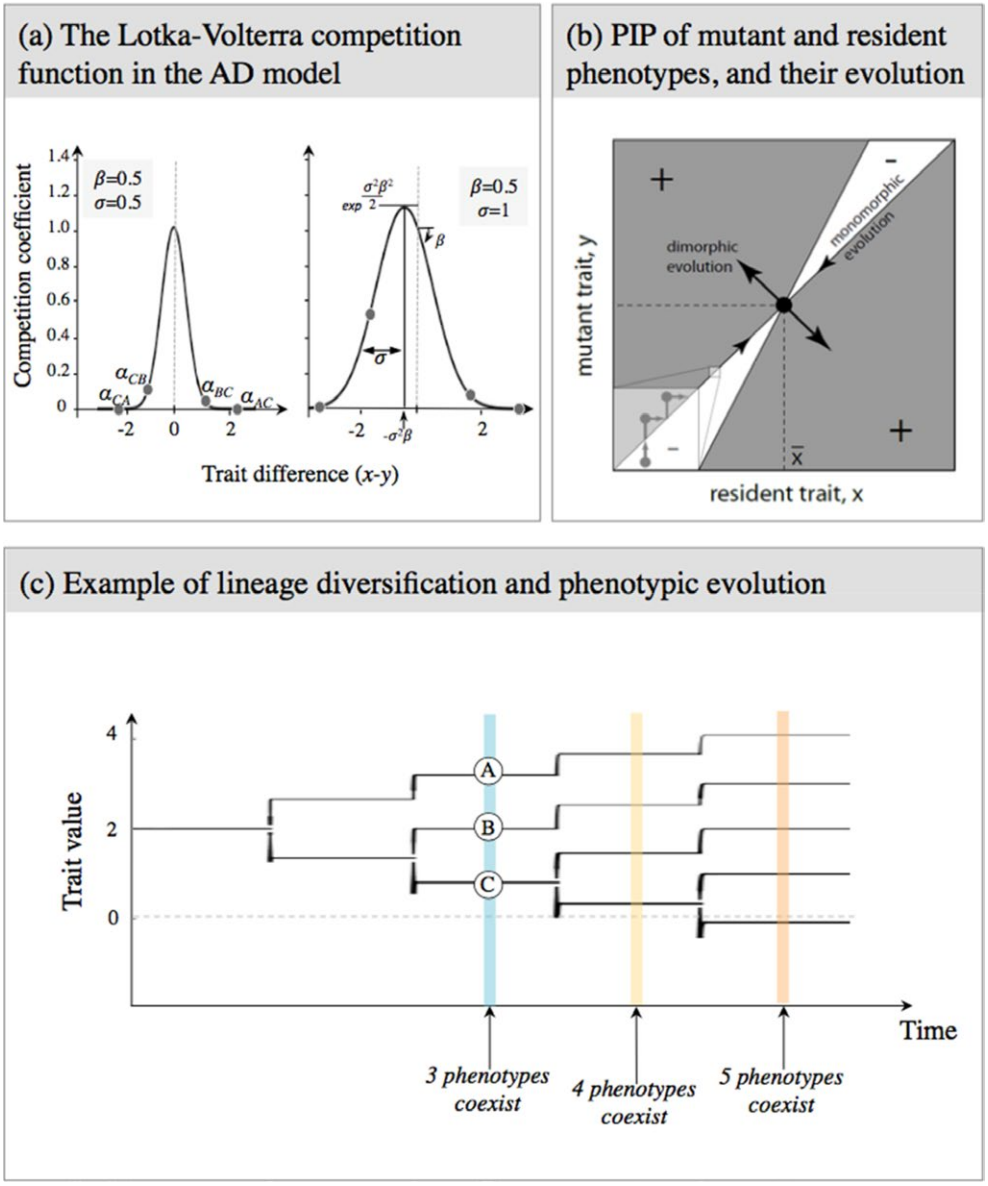

Figure Box. Illustration of the AD model (a) competition function, (b) pairwise invasibility plot (PIP) of the mutant and resident phenotypes and (c) lineage diversification pattern. (a) The competition between two phenotypes is a function of their trait difference. The function is characterized by two parameters, β and σ, describing asymmetry and strength of competition respectively. The left and right panels show two example functions that are characterized by the same value of asymmetry β = 0.5 but different values of competition strength σ = 0.5 (left panel) and σ = 1 (right panel). The dots on the curves represent the trait differences at the trimorphic equilibrium reached by evolution (highlighted in panel (c)), with $\alpha_{AB}=\alpha_{BC}$ and $\alpha_{BA}=\alpha_{CB}$ since traits are equidistant. (b) The PIP shows the signs and zero contour lines of the invasion fitness as a function of the resident and the mutant traits. Any mutant (grey dot in the lower left-shaded inset) in the negative (white) fitness region cannot invade the system and goes extinct. Mutants occurring in the positive (grey) fitness regions lead to resident-mutant substitution, and the mutant becomes the new resident trait (arrows pointing to the diagonal of the PIP) until the selection gradient (given by the difference in signs below and above the diagonal of the PIP) driving monomorphic evolution along the diagonal vanishes at the singular strategy (central black dot). At this point, the positive fitness curvature (given by the + signs below and above) indicates a fitness minimum, where mutants at both sides of the singularity can invade and coexist under disruptive selection (i.e. evolutionary branching, indicated by the arrows of the dimorphic evolution). (c) The diversification of a monomorphic lineage can lead to the coexistence of multiple phenotypes with different densities, ranging from high (thick lines) to low densities (thin lines). The three phenotypes at the trimorphic equilibrium are highlighted with the letters A, B, C, and their pairwise competition coefficients can be derived from the competition function in (a) as shown by the respective dots.

generated by varying the two key parameters of the model that define the asymmetry (β) and strength (σ) of competitive interactions. We used values of β and σ ranging from 0.1 to 1. We kept the carrying capacity function constant across simulations ($K_0 = 1$, $x_0 = 0$, $\sigma_k = 2$), initiated the simulations with a monomorphic population of trait $x = 0$ and simulated the trait adaptive dynamics until an evolutionary equilibrium with five lineages was reached. Although five lineages are obviously not the endpoint of evolutionary diversification, this choice allows us to explore whether, and if so then how, intransitive interactions change with increasing (odd and even) numbers of lineages, while at the same time, keeping computational effort and time reasonable.

2.2 | Identifying and quantifying intransitivity

Competitive interactions between multiple phenotypes may be of various forms, but they can always be ordered along a *transitive-to-intransitive* continuum, which ranges from strongly transitive to strongly intransitive interactions (Figure 1). To identify the position of the simulated coexisting lineages along this *transitive-to-intransitive* continuum, we designed an index which was inspired by Petraitis (1979)'s index (i.e. the minimum number of reversals required to transform an intransitive network into a transitive hierarchy). Our index aims to quantify any lack of strong transitivity in a system and relies on the **α** matrix of phenotype pairwise competition coefficients (α_{ij} representing the competition strength of species *j* on species *i*). From the **α** matrix, we estimate e_{ij}, the *normalized net competition effects* between each phenotype pair, as $e_{ij} = \frac{(\alpha_{ij} - \alpha_{ij})}{\max(\alpha)}$, where max(**α**) is the maximum competition coefficient of the **α** matrix. For instance, for three coexisting phenotypes {A, B, C}, strong transitive interactions occur when the net effect of A on C (e_{CA}) equals the net effect of A on B plus the one of B on C ($e_{CA} = e_{BA} + e_{CB}$). In contrast, a strong intransitive interaction occurs when the net effect of A on C is equal to the opposite of the net effects of A on B and of B on C ($e_{CA} = -e_{BA} = -e_{CB}$). Although it has been shown that the impacts of intransitive interactions on species coexistence are maximal when $e_{CA} = -e_{BA} = -e_{CB}$ (Gallien et al., 2017), various "weaker" interactions can occur when the interactions between phenotypes are neither strongly intransitive nor transitive (Edwards & Schreiber, 2010). Such a case, which we term *weak-intransitivity*, can for instance occur when the net effect of A on C is smaller than the sum of the net effects of A on B and of B on C (e.g. $e_{CA} < -e_{BA} = -e_{CB}$). In the context of our AD model, this situation can occur when the relationship between phenotype trait differences and competitive superiority is nonlinear. This would for instance occur when individuals with similar traits (e.g. shoot–root biomass ratio) show competitive interactions of greater strength than individuals with very dissimilar traits. The intransitivity of the indirect effect of competition among three phenotypes A, B and C is therefore calculated as follows:

$$IC = e_{AB} + e_{BC} + e_{CA} = e_{AB} + e_{BC} - e_{AC} \quad (3)$$

As *e* is standardized, it is bounded between -1 and 1, and thus, IC is bounded between −1 and 3. A value of IC ≤ 0 indicates transitive interactions, with increasing strength when IC tends to −1. A value of IC > 0 indicates intransitive interactions of strength ranging from weak (positive values close to 0) to strong when IC tends to 3 (Figure 1). Neutral coexistence between species would thus show an IC = 0 (all $e_{ij} = 0$), which is consistent since neutral coexistence is a transitive relationship. In communities containing more than three lineages, multiple intransitive loops may be present. In such a case, we use the average of this normalized index across all possible (three and more species) structures. It can be noted that two other metrics have been used in the past studies of intransitive interactions; however, none of them can detect early signals of weak-intransitive interactions (their focus being only on strong intransitivity as in Matías, Godoy, Gómez-Aparicio, & Pérez-Ramos, 2017; Soliveres et al., 2017 and Ulrich, Soliveres, Kryszewski, Maestre, & Gotelli, 2014 or on the impacts of intransitivity on coexistence as in Gallien et al., 2017 and Stouffer, Wainwright, Flanagan, & Mayfield, 2017).

With this index, we can evaluate whether the level of intransitivity obtained from in situ lineage diversification differs significantly from one obtained from a random assembly of phenotypes (e.g. similar to a random immigration from a regional phenotype pool). To do so, we compared the index scores observed at equilibria of the AD simulation to those obtained from 1,000 sets of randomly assembled phenotypes. Each random set was a random draw of phenotypes within the same trait interval as obtained from the AD simulations, and which can stably coexist on ecological timescales. Specifically, for each set of randomly drawn phenotypes,

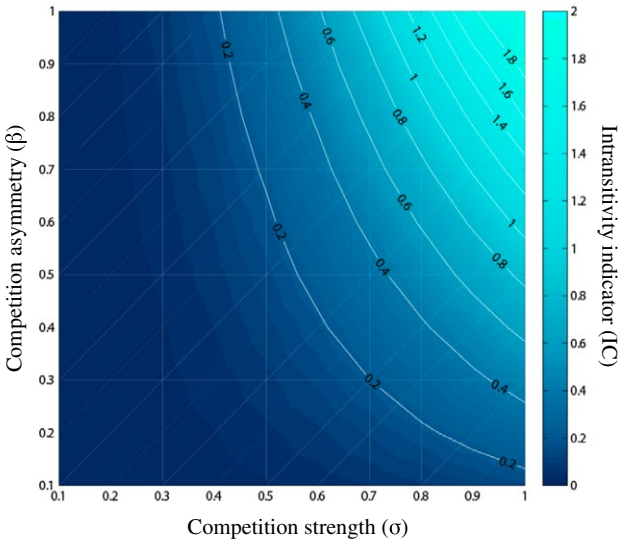

FIGURE 2 Influence of competition strength and competition asymmetry on the emergence of competition intransitivity for three coexisting phenotypes. The AD model relies on two key parameters: competition strength (σ) and competition asymmetry (β), which we varied to quantify their effects on the level of intransitivity once evolution has led to the diversification three distinct phenotypes (here studied at evolutionary equilibrium). Similar results hold for four and five coexisting phenotypes

we first evaluated whether they could all stably coexist under our resource competition model (equilibrium with all positive population abundances and negative real parts of all eigenvalues). We then selected only these sets of phenotypes that could stably coexist and calculated their degree of (in)transitivity with our index (IC, Eq. (3)). Notice that to compare the effect on intransitivity in assemblages emerging from sympatric evolution vs. allopatric remixing, we do not allow the phenotypes from these random draws to evolve further.

2.3 | Eco-evolutionary correlates of intransitive competition

By gradually increasing the strength (σ, varying from 0 to 1) and/or asymmetric competition (β, varying from 0 to 1) in our AD simulations, we generated a set of scenarios of lineage diversification and phenotypic disparification. These scenarios were used to investigate whether intransitive interactions can emerge during sympatric evolution and, if so, what the consequences would be for phenotypic diversity, stability and subsequent evolution. For each scenario, we quantified changes over time in terms of (1) the degree of intransitivity (once the system has reached three or more phenotypes), (2) the functional diversity of the coexisting phenotypes, (3) the ecological stability of their coexistence and (4) their evolutionary rates. The functional characteristics of the system were estimated by both the abundance-weighted mean traits of coexisting lineages and their average trait difference (as a measure of functional diversity). The (in)stability of lineage coexistence was estimated with both: a measure of the system invasibility and a measure of the system sensitivity to disturbances (i.e. the value of the real part of the leading eigenvalue of the Jacobian of the competition model). The system invasibility is estimated as the average invasion fitness over the entire feasible trait range (i.e. trait space ranging from −2 to 6), describing the expected growth rate of a random rare invader (Hui et al., 2016). The measure of sensitivity to disturbances depicts the rate at which the ecological system amplifies or dampens external perturbations; it is negative when lineages can coexist and becomes positive when stable coexistence is impossible. The evolutionary rates of the coexisting lineages were estimated with both the lineage origination rate (i.e. average rate of a new lineage emergence) and the rate at which new phenotypes diverge (hereafter called *divergence rate*).

3 | RESULTS

3.1 | Intraspecific weak-intransitive competition from sympatric diversification

Our index was designed to identify and quantify the degree of intransitivity in competitive interactions. We evaluated its performance on known competition networks reflecting different positions on the transitive-to-intransitive continuum (Figure 1). The index correctly distinguishes between transitive and intransitive interactions and can detect weak-intransitive cases (Figure 1). In the context of our simulations, the index values range from 0 to 2 (Figure 2), indicating that no strong intransitivity is reached by the system. In fact, species competitive interactions are determined by their phenotype along a single trait axis, and this prevents the emergence of strong intransitivity (see Section 4 for more details). However, both transitive and weak-intransitive interactions can emerge from this AD model.

With this index, the simulations of the AD model showed that once the initial monomorphic lineage has diversified into at least three distinct phenotypes, these three phenotypes interact in greater intransitive fashion as the asymmetry (β) and strength of competition (σ) increase (Figure 2). However, the impact of competition asymmetry (β) on the other indicators of the system (diversity, stability and evolutionary rates) is very limited (results not shown). Thus, for clarity of the discussion, from here on, we present only the results for a fixed competition asymmetry ($\beta = 0.5$) and varying competition strength ($0.1 < \sigma < 1$).

The simulations also showed that the mean level of intransitivity of the coexisting phenotypes increased with the number of phenotypes (from 3 to 5) and thus generally over time (since the number of lineage increases with time; Figure 3a). These temporal changes in intransitivity follow a pattern of punctuated evolution with a sharp increase when a new lineage originates followed by a stasis until another lineage is created (Figure 3a). These mean levels of intransitivity (for 3, 4 or 5 phenotypes) increase with increasing competition strength (σ; Figure 3b). In other words, an increase in the trait space on which a lineage has an influence via competition leads to the emergence of stronger intransitive competition in the system. Additionally, when competition strength is great enough, these mean levels of intraspecific weak-intransitivity emerging from in situ evolution become significantly higher than expected from the assembly of a random set of phenotypes (shaded areas in Figure 3b). Nonetheless, our indicator reveals an intransitivity score between 0 and 2 for all our simulations, which indicates that intransitivity in such system is significant but *weak* in its topology (competitive exclusion is not possible; see Figure 1). Indeed, all phenotypes can coexist in pairs, even the phenotypes with the highest and the lowest trait values (because competition strength decreases after a certain trait difference between phenotypes; see competition function in Eq. (1) and Box 1).

3.2 | Eco-evolutionary feedbacks in intransitive systems

To better understand the characteristics of polymorphic populations where phenotypes interact in an intransitive fashion, we explored three main eco-evolutionary properties: the trait diversity in populations, the ecological stability of their coexistence and the average evolutionary rates (Figure 4). As mentioned previously, for simplicity and given the negligible effect of β on most indicators, we here only present results for $\beta = 0.5$ and $0.1 < \sigma < 1$. Firstly, the results show that in systems containing greater intransitivity (and thus greater σ), the abundance-weighted mean trait across lineages decreases towards the resource optima $x_0 = 0$ (Figure 4a), while the average trait difference among lineages increases (Figure 4b). We also observed that increasing the number of lineages in the system (i.e. from 3 to 5 lineages)

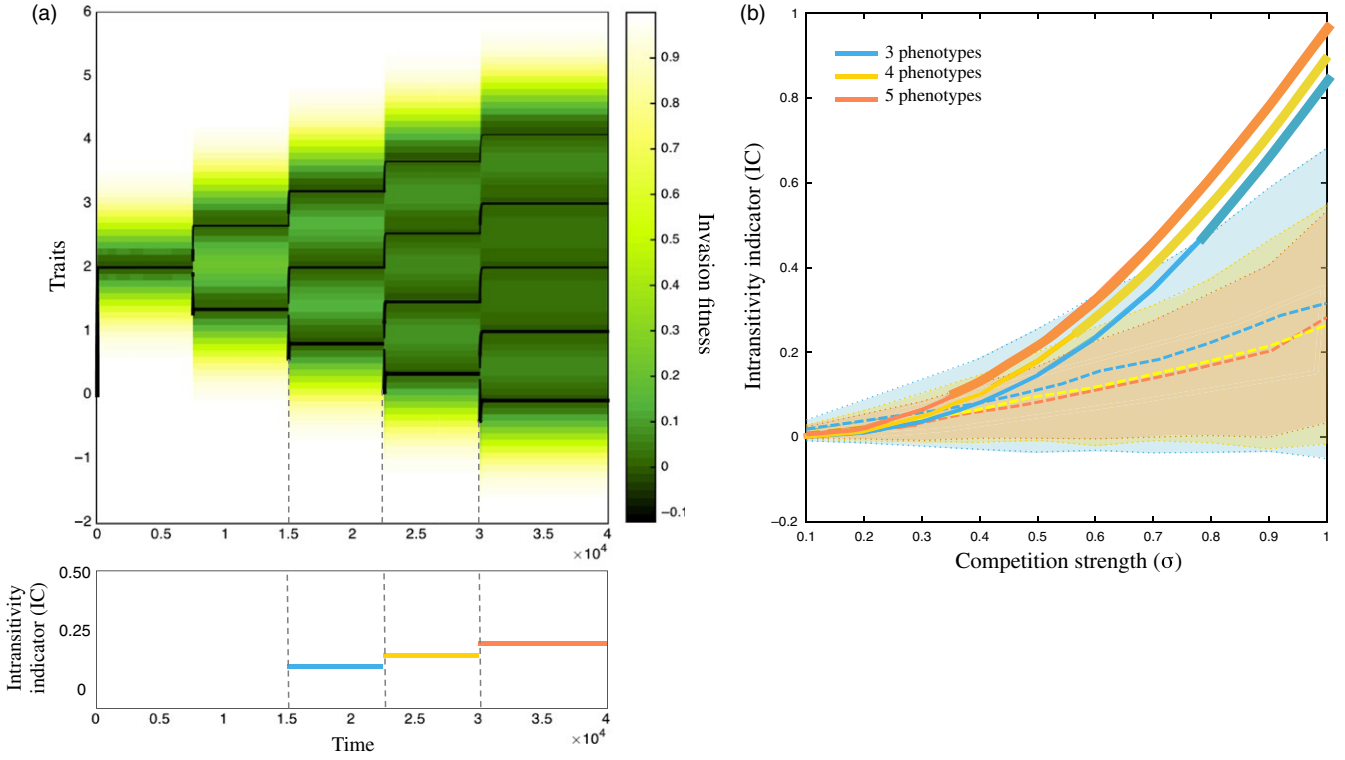

FIGURE 3 Phenotype adaptive dynamics and their degree of intransitivity. (a) Illustration of the adaptive dynamics of a lineage diversifying up to five morphs ($\sigma = 0.5$ and $\beta = 0.5$). Line thickness is proportional to morph density, background colour shows the *invasion fitness* of the trait landscape used to quantify the invasibility of the system and the lower panel shows the average intransitivity level over time (three phenotypes are indicated with a blue line, four phenotypes with a yellow line and five phenotypes with a red line). It can be noted that the simulations were initiated with the monomorphic lineage at $x = 0$, but this trait quickly evolved and centred on the monomorphic trait equilibrium (i.e. $\bar{x} = \beta\sigma_K^2 = 2$). (b) Relationship between the level of intransitivity (as measured by our indicator IC) and the competition strength simulated between phenotypes. The solid lines indicate the observed intransitivity from the AD simulations (same colours as in panel (a)). The dashed lines indicate the average intransitivity obtained from the assembly of a random set of phenotypes, and the respective shaded areas represent their confidence intervals

increased the coverage of the phenotypic landscape by these lineages (see Figure 3a), resulting in an increase in mean trait distance between phenotypes with lineage richness (blue to red lines in Figure 4b).

Secondly, we found an increase in the resistance of the system to invasion by new phenotypes as the strength of intransitive interactions and the number of lineages increased (Figure 4c). However, the stability of lineage abundances at equilibrium decreased with intransitive competition (as estimated with the leading eigenvalue of the Jacobian at equilibrium), indicating that the time necessary for disturbed lineages to return to equilibrium abundances is longer in systems with greater intransitivity (Figure 4d).

Thirdly, our results show that both the rates of lineage origination and the rates of lineage phenotypic divergence decrease strongly with increasing strength of intransitive competition (Figure 4e,f). These results were largely independent of the number of lineages considered.

4 | DISCUSSION

Our results show that *weak*-intransitive interactions can emerge at the intraspecific level from a single lineage diversifying in situ. These interactions, arising through disruptive selection for resource competition, are more intransitive than a random assembly of phenotypes when competition strength between species is high. Our simulations further show that populations with stronger intransitive competition also harbour higher functional diversity, are more resistant to invasion by new phenotypes but less resistant to disturbances and diversify at a slower pace.

4.1 | Emergence of intraspecific weak-intransitive competition via evolutionary branching

In the studied system, selection pressure for resource acquisition via asymmetric competition can lead to the emergence of weak-intransitivity. That is, for three coexisting lineages {A, B, C} of decreasing trait values, the competitive interactions are not transitive (which would be A > B > C, A ≫ C) but instead weakly intransitive: A > B > C ≈ A (where all pairs can coexist). This weak-intransitivity arises from great variations in the net competitive effect between lineage pairs, where the net effect of A on B and of B on C is much greater than the one of A on C (due to the large trait difference between A and C). Weak-intransitive systems have distinct properties

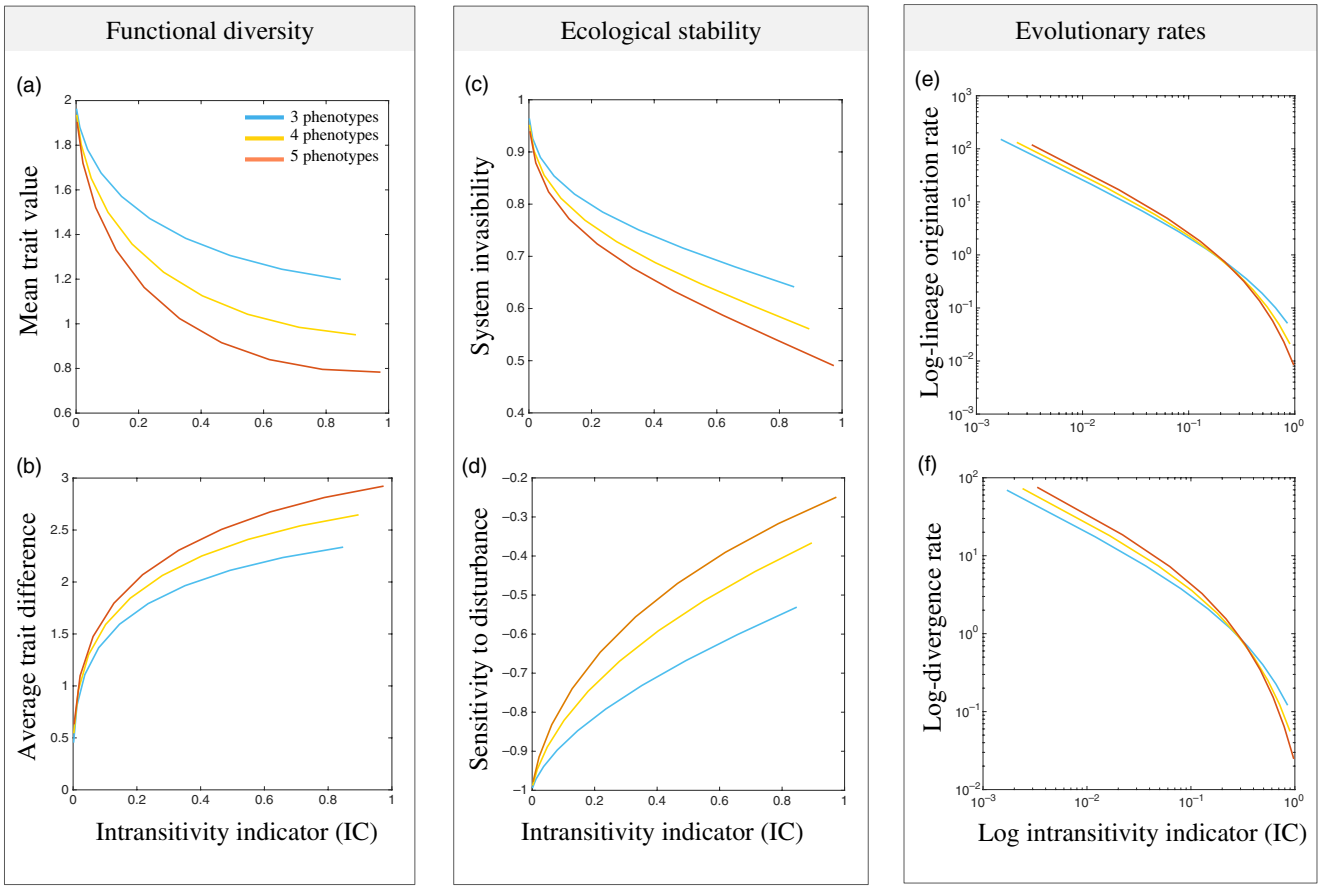

FIGURE 4 Relationships between the level of intransitivity and three main eco-evolutionary properties of the simulated system: (a–b) functional diversity, (c–d) ecological stability and (d–e) average evolutionary rates. The functional diversity is measured by (a) the abundance-weighted mean trait value and (b) the average trait difference between phenotypes. The ecological stability of the coexisting phenotypes is measured by (c) the invasibility of the system (as estimated with the mean invasion fitness of invaders) and its sensitivity to pulse disturbances (as estimated with the real part of the dominant eigenvalue of the system's Jacobian at equilibrium). The evolutionary rates are measured as (e) lineage origination rate (i.e. average rate of a new branching event) and (f) phenotype divergence rate (i.e. trait distance per unit of time); these relationships (e–f) are presented in a log–log scale to better visualise differences between numbers of phenotypes. The blue lines represent three phenotypes, yellow lines represent four phenotypes, and red lines represent five phenotypes

compared to strongly intransitive ones. On the one hand, a strongly intransitive system comprising an odd number of species/phenotypes can show negative frequency-dependent mechanisms that stabilize coexistence. On the other hand, if it is composed of an even number of species/phenotypes, it will generate positive frequency dependence mechanisms that destabilize coexistence (Allesina & Levine, 2011; Gallien et al., 2017; Vandermeer, 2011). These (de) stabilizing frequency dependence mechanisms can only occur when competitive interactions are arranged in a cyclic fashion (Gallien et al., 2017). Therefore, weak-intransitive systems may or may not embed such regulation mechanisms (see Figure 1). Indeed, in the case of our study species, interactions are not arranged in a cyclic fashion, which prevents frequency dependence mechanisms from occurring; this explains the monotonous trends observed when increasing the number of intransitive phenotypes (Figures 3 and 4). Our results also show that the level of intransitive interactions increases with the number of coexisting lineages. Indeed, when more lineages coexist, they occupy a greater functional space (due to limiting similarity processes) which allows for the emergence of longer intransitive loops of greater strengths (i.e. A > B > C > D > E ≈ A).

It is important to note that both transitive and weak-intransitive interactions are possible with this competition model. Transitive interactions arise when all pairwise competition coefficients can be located on the right hand side of the competition function maximum (i.e. all trait differences > $-\sigma^2\beta$), and intransitive interactions when at least one of them is located on the left hand side of the function maximum (i.e. trait difference < $-\sigma^2\beta$; see figure Box 1a). With the simulation model, we found that the strength of intransitive competition is very sensitive to σ, and thus to niche overlap between lineages (as niche overlap = $\exp^{\frac{-(x-y)^2}{\sigma^2}}$). Indeed, for a given trait difference between two lineages, increasing the niche overlap between them leads to stronger competition coefficients α_{ij} and thus to stronger net competition effects (e.g. e_{AB} and e_{BC} increase, while e_{CA} stays negligible; see Figure Box 1a). Thus, increasing niche overlap leads to an increase in intransitive interactions (see Eq. (3) and Figure 1). Moreover, increasing the asymmetry of competition (i.e. varying β

from 0.1 to 1) also leads to an increase in intransitivity. The competition asymmetry is evidently a necessary but not sufficient condition for the evolutionary emergence of weak-intransitivity, and weak-intransitivity can only emerge when the competition is also sufficiently strong. Together, these results show that weak-intransitive competition can emerge in any asymmetric system, even under moderate degrees of asymmetry, as long as competition strength is high enough.

Until now, the sympatric evolution of intransitive competition at the intraspecific level has been suspected but never documented in nature. For instance, in plant communities, Lankau and Strauss (2007) identified intransitive interactions between two genotypes of *Bromus nigra* and the other species of the communities, but whether these interactions could extend to three genotypes of *B. nigra*, and whether they evolved in sympatry or allopatry remains unknown (similar results were found for lizard and bacteria populations; Sinervo & Lively, 1996; Rainey & Travisano, 1998; Kirkup & Riley, 2004). Our modelling shows that, at least in the very simple conditions studied here (i.e. asymmetric competition along a single trait axis), intraspecific weak-intransitive interactions can emerge in sympatry through lineage diversification. Furthermore, if these diversification events occur together with reproductive isolation between phenotypes, then weak-intransitive competition may also evolve between sympatric species. This may typically occur in small isolated systems such as islands, mountaintops or lakes. Further investigation of intra- and interspecific intransitive interactions in such systems might therefore reveal that intransitivity is more frequent than expected in nature.

4.2 | Properties of intransitive systems

In the simulation scenarios favouring the emergence of intransitive interactions (i.e. high niche overlap), we found increased lineage functional diversity, mixed influences on the stability of coexistence and slower divergence rates (Figure 4). We now discuss possible reasons for these correlations.

4.2.1 | Greater functional diversity

As presented above, intransitivity increases with increased niche overlap between lineages (for given trait differences). Because of the negative effect of increased niche overlap, the resident phenotypes tend to reach their equilibrium abundances when they are more distant in the functional trait space. In other words, when the niche overlap between phenotypes increases, these phenotypes will need to evolve towards more different trait values in order to coexist. This leads to an increase in average trait differences with intransitivity (a result similarly observed in artificial fungi communities ; Maynard et al., 2017 but see Gallien, 2017). However, this increase in lineage trait divergence also leads to greater differences in the carrying capacities of different lineages (because of the competition trade-off, see Section 2), which overall leads to a decrease in the mean trait value of coexisting lineages when weighted by their densities.

4.2.2 | Mixed ecological stability

As expected from the positive relationship between intransitivity and functional diversity, a more strongly intransitive system is likely to be more resistant to invasion by an independent lineage (the average invasion fitness of other lineages is lower). This result indicates that in the context of our simulations, intransitive interactions can increase the stability of phenotype coexistence via niche filling. However, we also found that the resilience of the system in response to small pulse perturbation decreases with intransitivity and the number of coexisting lineages. This might be surprising at first since intransitive interactions among triplets of species or phenotypes are generally expected to have a stabilizing effect (Gallien et al., 2017; Vandermeer, 2011). The apparent contradiction between our result and the past literature is in fact due to the use of different concepts and approaches to quantify the stability of a system. Three main types of stability metrics can be differentiated: (1) measures of system invasibility by new phenotypes, (2) measures of recovery rates after small perturbations, and (3) measures of recovery rates after large perturbations. Our results suggest that increased intransitivity (1) prevents the establishment of new phenotypes in the system via niche filling (as measured by the system invasibility). Increased intransitivity further (2) reduces the system resilience after small pulse perturbations. This result is tentatively in agreement with May's *complexity begets instability principle* (May, 1972), showing that the probability of local stability in a community decreases with number of species and/or number and strength of interactions (Allesina & Tang, 2012; but see also Grilli, Barabás, Michalska-Smith, & Allesina, 2017). However, the exact mechanisms behind the complexity–stability relationship remain uncertain (partly due to the lack of analytical descriptions) and require further non-trivial investigations that are beyond the scope of our study (Landi, Minoarivelo, Brännström, Hui, & Dieckmann, 2018; Namba, 2015). Finally, previous work has shown that increasing intransitivity (3) enables a faster recovery after large perturbations of the system (where species abundance is reduced to few individuals) due to negative frequency dependence mechanisms (Gallien et al., 2017). Overall, the combination of these different results suggests that intransitive competition can have mixed impacts on community stability, and thus calls for more theoretical and empirical investigations.

4.2.3 | Slower divergence rates

Interestingly, although we found that more intransitive systems show higher trait diversity, the rates at which lineages branched and at which phenotypes diverged decreased. Indeed, when intransitivity increases, it takes longer for diverging phenotypes to reach their equilibrium abundances for two reasons: the traits at equilibrium are further apart in trait space, and the rate of trait evolution is slower. These properties are not directly driven by the increase in intransitivity. They are rather linked to the fact that when niche overlap between two phenotypes increases, then at the same time, not only their trait difference at equilibrium increases but also the selective pressure to diversify is decreased ($\sigma < \sigma_K$ in the monomorphic case).

4.3 | Limitations of the adaptive dynamics (AD) model

With this theoretical exploration of the evolution of intraspecific intransitive competition, we unravel the first elements of the eco-evolutionary triggers and impacts of this complex mechanism. However, we recognize that this is only a first step, and that building on these results with future studies will provide an enhanced understanding of how intransitive competition can emerge in nature, both at the intra- and interspecific levels. We now discuss some of our specific methodological choices, limitations of the AD model and perspectives of improvements.

4.3.1 | Model assumptions

The competition function is one of the key ingredients of evolution in our model. As already pointed out, it must be asymmetric and not monotonic in order to allow intransitive interactions to evolve (necessary conditions; Calcagno et al., 2017). However, the evolution of intransitivity is not guaranteed a priori by these assumptions (not sufficient conditions). Such an asymmetry and non-monotonicity of the competition function can, for example, be expected for competitive interactions mediated by plant height or animal body size, as observed in nature (e.g. Rall et al., 2012; Schneider, Scheu, & Brose, 2012).

The modelling framework of adaptive dynamics additionally relies on the assumption that homogenous populations evolve in a stable and isolated environment due to rare and small mutations that allow a separation of the fast ecological time-scale (assumed to be at its equilibrium) from the slow evolutionary time-scale. We also assumed that a single phenotypic trait is responsible for both resource exploitation and competition and ignored details of the genetic and sexual systems that could contribute to additional variability. Some of these assumptions have already been relaxed in theoretical studies, which have shown convergence of more complex dynamics to the simple adaptive dynamics used here (e.g. sexual reproduction with assortative mating in Dieckmann & Doebeli, 1999; and Geritz & Kisdi, 2000; and rarity of mutation in Meszéna, Gyllenberg, Jacobs, & Metz, 2005). More complex trait architectures may, however, be used to improve the realism of the simulations and thereby our understanding of intransitive eco-evolutionary feedbacks.

4.3.2 | Investigating intransitivity with other types of mechanistic models

To elucidate the conditions that can trigger or hamper the emergence of stronger intransitivity, two types of simulations models could be employed. Firstly, the evolution of stronger intransitivity in sympatry could be studied using multi-trait adaptive dynamics models (e.g. Falster, Brännström, Westoby, & Dieckmann, 2017). The presence of multiple trait dimensions could break the hierarchy of the single traits and should allow the evolution of strong intransitive (cyclic) competitive interactions. Such models would facilitate the investigation of the role of different types of trade-offs in the emergence of intransitive interactions. For instance, depending on the strength, direction and shape of functional trade-offs, it would be possible to test whether the time necessary for intransitive interactions to emerge depends on the level of phenotypic integration (Boucher, Thuiller, Arnoldi, Albert, & Lavergne, 2013; Schluter, 1996). Additionally, strong intransitive competition has a stabilizing effect on species or lineage coexistence when there is an odd number of lineages, but it has a destabilizing effect when there is an even number of lineages (Gallien et al., 2017). Therefore, the emergence of strong intransitive interactions in lineages composed of three phenotypes may prevent the evolution of a fourth phenotype (as it could destabilize the system).

From an ecological perspective, meta-community models (Hanski, 1998) could be used to investigate the emergence of intransitive interactions via immigration and local assembly of phenotypes. Until now, spatially explicit models have highlighted the influence of dispersal rate on the spatio-temporal dynamics of intransitive interactions in spatially structured landscapes (e.g. Reichenbach et al., 2007; Schreiber & Killingback, 2013; Zhang et al., 2006). Reichenbach et al. (2007) notably showed that when species dispersal rates are too high, then intransitive coexistence is no longer stable and one species will dominate the system. Similar analyses could further be used to investigate how disturbance regimes (such as climatic fluctuations or general climate warming) complicate or facilitate intransitive coexistence.

5 | CONCLUSIONS

Intraspecific weak-intransitive competition can emerge during sympatric lineage diversification even with limited asymmetry in competition along a single trait dimension, provided competition strength is sufficiently high. Our results now call for more empirical investigations of intraspecific intransitivity on both ecological and evolutionary time-scales in order to explore the emergence of intransitivity via plasticity and character displacement, and the evolution of intransitivity in isolated systems (such as islands or mountain tops) respectively.

ACKNOWLEDGEMENTS

We thank Florian C. Boucher for discussing and commenting on early versions of the manuscript. Our work also greatly benefited from the constructive suggestions of the associate editor and two anonymous reviewers. We acknowledge support from the DST-NRF Centre of Excellence for Invasion Biology and the National Research Foundation of South Africa (grant 85417 to D.M.R.; grants 89967 and 109244 to C.H.).

AUTHORS' CONTRIBUTIONS

L.G. and P.L. conceived the study. P.L. built the model and ran all simulations, which L.G. and P.L. analysed. L.G. and P.L. wrote the

first draft of the manuscript which was significantly improved by C.H. and D.M.R.

DATA ACCESSIBILITY

This manuscript does not use original data. The main modelling script (in Matlab) is available to download from Dryad Data Repository: https://doi.org/10.5061/dryad.q3sh7 (Gallien, 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Gallien L, Landi P, Hui C, Richardson DM. Emergence of weak-intransitive competition through adaptive diversification and eco-evolutionary feedbacks. *J Ecol*. 2018;106:877–889. https://doi.org/10.1111/1365-2745.12961